NEW ABERRATION OF *PYRONIA TITHONUS BRITANNIAE* (L.) (LEPIDOPTERA: NYMPHALIDAE) AND ITS DEVELOPMENTAL BASIS

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Abstract

An example of *Pyronia tithonus* with corresponding upperside and underside symmetrical white blotches, but which does not conveniently fall into any defined category of aberration, is described. The pattern formation processes affected, and the possible environmental and genetic causes, are considered.

Observations

On 5th July 2003, while collecting *Thymelicus* butterflies (Hesperiidae) at Southampton University's conservation area at Chilworth, Hampshire vice-county 11 (SU4018) for a study into species recognition by computer, my attention was drawn by a specimen of the Gatekeeper *Pyronia tithonus* (L.) with a prominent white blotch on the hindwing undersides and which I therefore retained. It required some coaxing to open its wings, when I noticed a similar blotch on the hindwing uppersides but could not discern any forewing sex brands. Its abdomen was distinctly slender, but as the claspers were also hard to discern and its worn condition suggested an older individual, I could not reliably exclude the possibility of it being a largely egg-depleted female which might yet yield some ova. I had attributed its small size to its aberrant nature, and only after observing typical females flying locally did I re-examine it, confirm it was male, and decide to set it (Plate 15, Figs 1a and 1b). It was shown at the BENHS Annual Exhibition 2003.

Superficially, it is closest to ab. *postalba* aberrations in which the hindwing orange ground colour is replaced symmetrically by pure white (Leeds, 1949), and as with many comparable aberrations (Russwurm, 1978; Harmer, 2000) both surfaces are affected. However it also shows features of *partimtransformis* aberrations in which the pale patches do not conform to the marking boundaries and are less perfectly symmetrical (Leeds, 1949). On the hindwing uppersides, the white coloration obscures the eyespot ring in s2 and in s1–3 extends as a suffusion onto the darker basal area, while in s4 some of the ground colour remains unobscured (Plate 15, Fig. 1a). The forewing uppersides have an asymmetrical white suffusion on the sex brand in s1b–3, and in s3 some pale scaling below the twin eyespot. The eyespot is itself unusually large, adding to the specimen's female-like appearance. These features are repeated in corresponding positions on the underside (Plate 15, Fig. 1b). The aberration does not fall conveniently into any of the categories described by Leeds (1949), Russwurm (1978), Harmer (2000) or Carter *et al.* (2004), and may be unique.

The nature and location of abnormalities can help identify their causes. *Pyronia tithonus* lacks the flavonoid pigments of some Satyrinae (Ford, 1957) and as in other Nymphalidae the matt white of the eyespot pupils is structural (Scoble, 1995). These are distinguishable from the pale patches which appeared translucent when held up to the light. Examination with a hand lens revealed these to be thinly scaled, with the scales themselves ranging from almost white to very pale grey, and a more obvious grey on the normally darker-brown wing areas. The orange and browns replaced by the pale patches are produced by melanins (Nijhout, 1981). Pigment synthesis occurs within

the wing-scales as enzymes lodged in their cuticles interact with pigment precursors circulating in the haemolymph (Nijhout, 1980). The precursors are produced sequentially. In one model, scales within each colour area possess just one enzyme and can process just one precursor. In the other model, every scale has the full set of enzymes, but each substrate can only access scales of a given maturity and so the visible pattern reflects the initiation sequence or rate of scale development. The fact that the colours replaced by the pale patches appeared normally in their other locations rules out a global mutation in a gene coding for a pigment substrate or enzyme. Yellows and greys too are produced by melanins (Nijhout, 1981), and variations in the intensity of melanin-related colours can also arise from differences in their concentration (Nijhout, 1980). The abnormal coloration is therefore most likely due to a defect in the development of scale structure that interfered with the incorporation of melanin-synthesising enzymes in their cuticles or access to them by their substrates.

Bilateral symmetry is established early in egg development (Goodwin, 1984), at which time left and right sides become independent. The imaginal discs from which each wing develops comprise developmental units or 'compartments' (Sibatani, 1980) and start growing around the time the larva hatches (Nijhout, 1995). From the outset, the anterior compartments of both wings function as one collective unit and their posterior compartments as another. Their boundaries correspond to the borders of s5/s6 (Sibatani, 1980) and in the hindwings of some Satyridae possibly s4/s5 (Winokur, 1996). Upperside/underside independence (with the anterior and posterior of both wings still functioning collectively) then arises in early imaginal disc development, and finally forewing/hindwing independence is established (Sibatani, 1980). The positions of the pale patches thus indicate that they are confined to the posterior compartments, and their strong upperside-underside correspondence but poorer symmetry (Plate 15, Figs. 1a–1b) indicates that their ultimate cause can be traced back to an event occurring after the establishment of left/right independence but before the attainment of upperside/underside independence.

Despite the assertions of Windig & Nylin (1999), Lepidoptera do not exhibit directional symmetry or antisymmetry (where asymmetry is the rule but unpredictable in direction, Soulé, 1967), and the imperfect left-right correspondence is attributed to random non-directional 'fluctuating asymmetry' (FA). FA is a manifestation of the perturbation of developmental pathways, and its magnitude indicates how well they are buffered against this (Mpho *et al.*, 2000). Buffering ability can have a genetic basis though the genes involved need not be the ones responsible for producing the phenotypic trait in question (Reeve, 1961). Sources of perturbation include environmental stresses and genetic imbalances (Mpho *et al.*, 2000). Thus aberrant individuals and traits can be expected to show a higher than usual level of fluctuating asymmetry (Soulé & Baker, 1968), and this is consistent with the more perfect symmetry of the specimen's non-aberrant features.

It is not possible to tell from its appearance whether the aberration had a genetic or environmental basis because both kinds of factor can exert equivalent influences on patterning physiology. Indeed environmentally produced phenotypes often resemble known genetic or geographical forms, when they are described as 'phenocopies' (e.g. Tebbutt, 2002), though neither gene nor environment can be considered primary in the production of the common phenotype (Goodwin, 1988). Furthermore, susceptibility to environmental modification can itself have a genetic basis, with the resultant phenotypes disclosing this underlying genetic variation (Nijhout, 1984). As with 'classical' genetic traits this variation can be continuous (Nijhout, 1984) or discontinuous (Bailey, 2002) in its expressivity. The summer of 2003 was exceptionally warm and would have been conducive to the production of environmental variants.

Sensitive times include the late larva to early pupa when imaginal wing-disc growth is complete (Nijhout, 1985) and the late pupa when scale maturation and pigment synthesis are ensuing (Nijhout, 1991). In *P. tithonus* these stages correspond to the middle weeks of June and to mid-July to early August (Thomas & Lewington, 1991), though the warm spring had advanced many species by up to three weeks.

Alternatively, the warmer weather could have enabled the survival of a deleterious genotype that would otherwise have perished in an immature stage. A generally improved survival of immatures would also increase the likelihood of a rare genotype appearing in the adult population simply because individuals are more numerous (Ford, 1957), though hot dry summers do tend to shorten adult life span in the species (Asher *et al.*, 2001).

Given the occurrence of the Gatekeeper aberration at the site, it is notable that an ab. *marconi* Frohawk of the Marbled White *Melanargia galathea* (L.) (Russwurm, 1978) was seen (and photographed) there nine days later by Dr James W. Peat of Southampton University (pers. comm.).

It would have been desirable to pair the aberration with a virgin female to determine its genetic basis, though experiments on other species using artificially bleached specimens suggest it would be less attractive to mates (Ford, 1957). A genetic basis would require either a pre-existing gene or a newly arisen mutation. If due to a pre-existing gene then it would almost certainly be recessive, because a non-deleterious dominant would be expected to have been manifest in more individuals, while an ancestral deleterious dominant would become lost from the population or rendered recessive by evolution (Ford, 1957). In the latter case the aberration would be homozygous, and when backcrossing the F_1 heterozygotes should yield 25% homozygote recessives in the F_2 (Harmer, 2000). Since the proportion of heterozygotes in a population can be high even when the recessive homozygote is rare (Falconer, 1981), future observations at the site could also prove informative. If due to a newly arisen mutation, the chance of the mutation occurring in both alleles at the gene locus is so vanishingly small that the aberration can be considered heterozygous and hence dominant. Here, pairing with a wild-type female should produce 50% aberrants in the F_1. In both cases, a significantly lower than expected proportion would imply deleterious pleiotropic effects. However, even a dominant aberration may fail to appear among the F_1 adults if it is highly deleterious. Genetic loads in Lepidoptera mainly concern the metabolic integration of the individual and mostly manifest as death of the developing larva within the egg (Oliver, 1981). In this event, the frequency of aberrant genotypes among the F_1 might instead be estimated from the proportion of eggs failing to hatch; though failure of an entire egg-lay is usually indicative of a lack of insemination (Oliver, 1981).

Rearing under different temperatures and humidity regimes can reveal how seasonal conditions affect the fitness of aberrant genotypes, while pairings between individuals of given responsiveness to temperature 'shocks' and examining the expressivities of their F_1 under corresponding treatment, can help determine the role of genotype in conferring susceptibility to environmentally-induced pattern modification (Waddington, 1942; Shapiro, 1981).

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BOOK REVIEW

The Aculeate Hymenoptera of Wales. With special reference to the manuscript 'The Aculeates of Wales' by H.M. Hallett. By Mark Pavett and Adrian Fowles. 120 pp. Obtainable from Department of Entomology, National Museum of Wales, Cathays, Cardiff CF10 3NP. Price £5.00, £7.00 p&p.

This, the first in the 'Biotir' series of publications produced by the National Museum of Wales, aims to increase the availability of the information stored within the museum. As a first production it does this job very well, which is a good thing, or H.M.H. would be turning in his grave. He put an awful lot of time and money into the Cardiff Museum and must have been keenly upset to see the relative disregard with which Natural History was held during his lifetime. As anybody who has been to the modern entomological section of the museum as part of a BWARS meeting, or for any other reason, will have seen, he has at last been satisfied; the Biodiversity and Systematic Biology (Natural History!) Department now has the room and staff to become not only a museum for Wales, but also the world.

H.M. Hallett apparently always intended to write-up and publish the Aculeate Hymenoptera of Wales, but, understandably, his wish to see it as complete as possible meant that he was never satisfied. Hence, the manuscript account which forms part of this publication is as far as he ever got. Not that this was an insignificant effort, not only in its geographical coverage, but also in the notes he made concerning the species recorded. In this it matches several long-quoted papers (on *Andrena* and *Nomada*; *Halictus* and *Sphecodes*) by R.C.L. Perkins and it is very useful to have a second opinion on the status of aculeates which is largely based on a different region of the UK. He agrees with Perkins in his assessment of *Lasioglossum nitidiusculum* (Kirby) as being common – oh where is it now! He also found *Andrena flavipes* Panzer almost unknown in Wales, although he knew it to be abundant elsewhere. Interestingly it now is common, in southern Wales, at least!

Mark and Adrian have updated the overall Welsh list by reference to their own and other collectors' records and by thoroughly going over all the material held in the museum. In the current publication, supplementary lists give those species which Hallett should have been aware of, but which never made it to the manuscript, and those species added to the Welsh list since Hallett's time. Inevitably anyone with direct knowledge of the area, or species, in question will have their own quibbles – what happened to the record for *Hylaeus signatus* (Panzer), taken by Mark and myself on Merthyr Mawr in June, 1998? I would also dearly love to see the specimen on which the record for *Ammophila pubescens* Curtis is based. However, these thoughts just serve to emphasise the value of the work. No longer does one have to go to Cardiff: Mark and Adrian have brought Cardiff to you, and all for a very modest sum. I urge all with an interest in Aculeates to rob their piggy banks and get a copy.

MIKE EDWARDS